The impact of soil organisms on soil functioning under neotropical pastures. A case study of a native anecic earthworm species

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Abstract

The description of main biological, ecological and functional attributes of a native earthworm species in a natural savanna and several introduced pastures from the Eastern Plains of Colombia was the main objective in this study. To achieve this a set of different experiments and explicit field work were designed and carried out at the Carimagua Research Station, 320 km east from Villavicencio (Meta department).

Martiodrilus n. sp. (Oligochaeta, Glossoscolecidae) is a large native earthworm from the natural savannas of the eastern plains of Colombia. It inhabits semi-permanent U-shaped burrows at the entrance of which individuals deposit superficial and tower-like casts of very large size. A strongly positive correlation was observed between the number of fresh casts and the number of individuals collected in the first 10 cm of soil during the active period of this species ($r= 0.907$; $P < 0.01$).

Density and biomass of this species were significantly much higher in the introduced pastures compared with the savanna (ANOVA, $P < 0.01$). The cocoons are ovoid in shape and rather large (23.6 x 14 mm, and almost 20% of adult weight), from which two individuals emerge. Evidence of vertical migration during the year was observed, while it is active in the topsoil during the beginning of the rainy season, it enters in a true diapause to withstand adverse environmental conditions before the onset of the dry period, being adults the .

This species selected food substrates with high organic contents since casts produced in the two systems had significantly higher total C contents and total N than the bulk soil. C contents also increased significantly during cast ageing (+ 100%), possibly because of CO_2 fixation processes, dead root accumulation and/or macrofaunal activities in casts.

Another experiment was conducted to determine the effects of earthworm activities on soil and cast seed banks. The composition of the above standing vegetation was relatively closer to that of the cast seed bank than that of the soil seed bank. This may be due to the presence of enhanced conditions for germination in surface casts, which may increase the chances for egested living seeds to germinate and contribute to the plant cover.

The results obtained in this study support the general knowledge of how earthworms can affect soil fertility and plant growth. Martiodrilus n. sp., through the production of casts affects the availability and nature of both the spatial and trophic resource in soil. This species certainly belongs to the functional group of "ecosystem engineers", as it affects the availability of some resources for other organisms through the production of physical biostructures. The next step in research should be directed now to test whether Martiodrilus n. sp. is a keystone species within the soil community or not.

Keywords: Earthworms, Biodiversity, Soil functioning, Pastures, Savannas, Ecosystem engineers, Functional ecology.

1. Introduction

The savannas of the eastern plains of Colombia occupy some 17% of the national area (16.9 million ha) and mainly consist of poor nutritive quality herbaceous vegetation where extensive cattle grazing occurs (Vera and Seré, 1985; Álvarez and Lascano, 1987). The substitution of the native savanna by introduced grasses from Africa has been a widely accepted practice in the Colombian "Llanos" and in the Brazilian savannas or "Cerrados" during the last 20 years in order to increase the proportion of land used for more intensive food production. Improved pastures based on introduced grasses from Africa, principally Brachiaria spp., and Panicum spp., with or without forage legumes, e.g. Stylosanthes sp., Arachis sp. and Pueraria sp., and annual crops with inputs of fertilizers and lime, mainly upland rice and soybeans, are land management options normally found in these areas. As a result there has been a rapid increase in agricultural production but the long term sustainability of these agroecosystems is limited. In addition, we know little about biological processes involved in these land use changes and how these can alter fundamental ecosystem processes and services, especially when it is evident, from studies carried out in the Brazilian "Cerrados", that biodiversity of the neotropical savannas is more threatened than that of the Amazon forest (Smith et al., 1998).

The study of diversity and ecological processes linked to ecosystem functioning constitute the basis for an understanding and better management of natural and derived ecosystems (Giller, 1996). Communities of soil fauna are, in general, sensitive to climatic and edaphic factors which in turn determine the availability of food resources and microclimatic conditions. Besides, human-induced disturbance of natural ecosystems will

alter the macroinvertebrate communities in the soil (Decaëns et al., 1994; Fragoso et al., 1999).

Earthworms are the most abundant group of macrofauna in the soil in terms of biomass and they generally participate in the regulation of important soil processes through their functional domains (Lavelle, 1997). The effects of earthworms on soil physical properties, nutrient dynamics, organic matter and plant growth has been studied in detail (Aina, 1984; Casenave and Valentin, 1988; Shipitalo and Protz, 1989; Blanchart et al., 1993, 1999; Sharpley and Syers, 1976; Barois et al., 1987; Martin, 1991; Brown et al., 1999). However more effforts are needed to evaluate the role of the biogenic structures produced by theses organisms in soil functioning and ecological processes.

The substitution of the natural ecosystem (native savanna) by introduced pastures influences the functional structure of the earthworm communities although species richness is the same (Jiménez et al., 1998a, b). Andropogon gayanus and Brachiaria decumbens, alone or in association with the forage legume Pueraria phaseoloides, Brachiaria humidicola, alone or in association with Arachis pintoi or other legumes are systems that conserved the native macrofauna at Carimagua. These results are exceptional as disturbances to natural systems result generally in a decrease or disappearance of the native species. Normally, pantropical species with a wide range of tolerance to physico-chemical properties (peregrine species) such as Pontoscolex corethrurus Müller and Polypheretima elongata Perrier (Barois et al., 1988; Lavelle and Pashanasi, 1989; Barros et al., 1998; Fragoso et al., 1999) become predominant.

Of the innumerable life forms that inhabit soils only a small number of macroinvertebrates (earthworms, termites and ants) are capable to plow soil and produce a large variety of organo-mineral structures, e.g. nests, mounds, macropores, galleries and

excretions. These organisms are named “ecological or ecosystem engineers” (Stork and Eggleton, 1992; Jones et al., 1994) of the soil and their structures have been described as “biogenic structures” (Anderson, 1995; Lavelle, 1997, 2000).

In agreement with the high species richness of the savanna (Decaëns et al. 1994) a high functional diversity exists in Carimagua, in terms of different biogenic structures. Fourteen types of these structures are produced by the ecological engineers, i.e. 4 termite structures, 8 types of ant nests and 2 types of earthworm casts on the soil surface (Decaëns et al., 2001). It is on one of these biogenic structures and the species that produce them, the anecic Martiodrilus sp. (Glossocolecidae, Oligochaeta) where the research presented here has been focused on. These surface casts are formed by a continuous deposition of egested material at the opening of the burrow during several days. The final structure is a towerlike cast (Picture 1) with a fresh pasty structure in the top and dry material at its base easily recognisable from other soil surface casts. The term towerlike was prefered although it was originally created to describe casts of Hyperiodrilus africanus (Madge, 1969). When the earthworm Martiodrilus sp. leaves its semi-permanent U-shaped burrow or when it sinks to start diapause (Jiménez et al., 1998a) the cast dries completely. Dry casts remain at the soil surface for more than one year after having been egested, and the disappearance of casts is mostly attributed to rainfall drop impacts (Mariani et al., unpublished) and to cattle trampling in the grazed pastures (see Decaëns, 2000 and Decaëns et al., 1999a, for more details).

The functional role of these structures is believed to be of utmost importance and represent sites where certain pedological processes occur such as the stimulation of microbial activity, the formation of soil structure, the dynamics of soil organic matter or the

exchange of water and gases (Anderson, 1995; Lavelle, 1996; Beare and Lavelle, 1998). In this study our objective was to assess some ecological processes at the scale of the biogenic structure and relate them with the living habits of the species. C and N dynamics and the effects on soil seed banks in surface casts of Martiodrilus sp. were the main studies adressed in this paper.

2. Materials and methods

2.1. Study site

The study was carried out at the "Centro Nacional de Investigaciones" Carimagua (CIAT-CORPOICA agreement), in the well-drained isohyperthermic savannas of the Eastern Plains of Colombia (4° 37' N and 71° 19' W, 175 metres altitude). Climate is subhumid tropical with a four month dry period from December to March and an average yearly rainfall and temperature of 2280 mm and 26°C, respectively (1972-1995, CIAT data). Vegetation is characterised by open herbaceous savannas with scattered trees and bushes in the uplands ("altos") and gallery forests and palm trees ("morichales") in the low-lying savannas ("bajos"). Burning is used to get rid of excess vegetation and to stimulate the re-growth of those more nutritional plant material (Rippstein et al., 1996). Soils at the study site are Oxisols (Tropeptic Haplustox Isohyperthermic) in the uplands and Ultisols (Ultic Aeric Plintaquox) in the lowlands (USDA). These soils are characterized by their acidity (pH 4.5, water), a high Al saturation (> 80%) and low concentrations of exchangeable Ca, Mg and K. Phosphorous is a limiting nutrient for plants as it remains

fixed by Al in stable compounds, what reduces the productivity of these acid soils (Walker and Syers, 1976; Rao et al., 1999).

All the research was done on the same upland edaphic unit (pedon Carimagua) where different plots were located: A native savanna without grazing nor burning where Andropogon bicornis and Gymnopogon sp. were the predominant plant species, and a grazed pasture, in a two ha plot, that combines an exotic African grass, B. decumbens cv. Basilisk, and a tropical herbaceous legume, P. phaseoloides CIAT 9900 ("Kudzu"). Cattle stocking rates are 1 animal unit (AU) ha^{-1} in the dry season and 2 AU ha^{-1}in the wet season (1 AU = 250 kg live weight).

2.2. Earthworm population sampling

With the objective to assess the biology, ecology and population dynamics of species across time a stratified sampling procedure was performed during 17 months. Physical methods of extraction were applied to collect earthworms. These are often very tedious, hard working and time consuming. From April 1994 to September 1995 earthworms were hand-sorted from five 1 m^2 soil monoliths, following Lavelle (1978), monthly. A trench was dug around the monolith to avoid earthworm escaping and ease the separation of 10 cm sucessive layers. Normally, five soil layers were revised, till 50 cm. However, as some species migrate deeper into the soil, e.g. Martiodrilus sp. (Jiménez and Decaëns 2000), sampling depth varied accordingly. Vertical distribution was not much affected by sampling since a positive correlation between the number of fresh casts in the soil surface and the number of earthworms in the topsoil exists (Jiménez et al., 1998a). Soil blocks were

carefully hand revised and all earthworms and cocoons collected. Whether any earthworm was in dormant stage, i.e., quiescence or diapause, or not is annotated.

All earthworms were carried to the laboratory where complete specimens were weighed and the maximum preclitelar diameter measured in fragmented worms, since it has been very useful to estimate the weight of the complete earthworm (see Jiménez et al., 1998b and Jiménez et al., 2000). Biomass is based on formalin preservation, 12% lower than fresh weight on average for Martiodrilus n. sp. (Jiménez et al., 2000).

2.3. Sampling of biogenic structures

2.3.1. Experiment I: C and N dynamics in casts

This experiment was carried out in two grazed pastures (2.0 AU. ha^{-1}): (1) A 3 year-old pasture of B. humidicola (Rendle), A. pintoi Krap & Greg, S. capitata Vog.and Centrosema acutifolium Benth; (2) A one year-old pasture of P. maximum and A. pintoi.

During the peak of earthworm activity of this species, at the onset of the rainy period (May 1996), and with the soil surface of pastures almost completely covered by these casts, an experimental approach was initiated. 160 surface casts of Martiodrilus n. sp. were gathered into 4 groups (40 neighbouring casts in each group) and individually identified with small metal plates. Only fresh and yet small casts were chosen at this stage. By this procedure we ensure the early phase of cast deposition and earthworm presence in each of the marked casts. Any cumulative effect of cast material is then avoided. In the pasture, each group of casts was protected from animal trampling by a 2 x 2 m metallic wire cage. Samples were taken at different dates: 1, 2, 3, 7, 14 days and 1, 2, 5, 6.5, 8 and 11 months

after deposition of the casts. Each date a sample was randomly taken from each group of 40 casts and it consisted of: (i) one cast, (ii) the underlying soil (located directly below the cast) and (iii) the adjacent soil (located 20 cm away from the cast). Samples were carried to the laboratory in an ice chest to preserve them from further mineralization processes.

Total C and N were analysed on previously 2-mm sieved subsamples. A colorimetric method after acid digestion was used to measure total C contents (Houba et al. 1988), and the standard Kjeldahl digestion for total N (Krom 1980). Ammonium and nitrate concentrations were determined by colorimetric methods (Anderson and Ingram 1993).

2.3.2. Experiment II: cast and soil seed banks

Three experimental plots were selected to compare native savanna with different pastoral systems under study at the research site (Friesen *et al.* 1997):

(a) A Paspalum pectinatum Nees, Axonopus purpusii (Mez.) Chase, and Trachypogon vestitus Anders. native savanna, protected from grazing for four years and traditionally managed by fire during each dry season.

(b) An 18 year-old associated pasture of B. decumbens Stapf. and P. phaseoloides Benth. (pasture A), grazed by cattle and maintained with a stocking rate of 1.0 animal unit. ha^{-1} during the dry season and 2.0 animal units. ha^{-1} during the wet season.

(c) A 3 year-old associated pasture of B. humidicola (Rendle), A. pintoi Krap & Greg, S. capitata Vog. and C. acutifolium Benth. (pasture B), grazed by cattle with an average stocking rate of 2.0 animals units. ha^{-1}.

The field work was initiated in August 1996, i.e. at the middle of the rainy period. Our idea was to take samples from the permanent soil seed bank, assuming that most of the

temporary seed banks had already germinated at the onset of the rainy season. Twenty soil cores (8 cm diametre and 6 cm depth) were taken in each experimental plot and 300 fresh casts were randomly collected. Both soil and casts were air-dried for 15 days and weighed.

Each sample was put on a 2-cm layer of river sand in a plastic seed tray (26x27x6 cm). Soil layers were less than 5 mm in order to allow the germination of the larger part of the seeds (Dalling et al., 1994). Forty trays were used for each plot (20 for each type of sample, i.e. soil and casts) and 10 trays were filled up with sand alone and used as control. Germination trays were located randomly in a greenhouse, kept moistened and exposed to natural light and temperature regimes (approximately 12h/12h darkness/light and 26 °C, respectively). Once a week, the emerging seedlings were identified at the species level and removed. After three months, casts were broken in small fragments (< 5 mm of diameter) before being placed in the trays to continue the evaluation. For each sample, 40 g of dry soil or casts where randomly taken at the beginning of the experiment. Each sample was soaked for a minimum of 30 minutes in a solution of sodium hexametaphosphate (50 g. l^{-1}) and sodium bicarbonate (25 g. l^{-1}). Afterwards, the suspension was poured through a 0.125-mm sieve. Organic debris were washed with a fine spray of water and oven-dried for 48 hours at 70°C. Both damaged and undamaged seeds (i.e. seeds which visually seemed to be intact and resisted gentle pressure) were separated under a stereo-microscope and counted.

2.6. Statistics

Simple linear regression analysis (Pearson *r*) was used to study the correlation among variables. Analysis of variance (ANOVA) was employed to test for significant differences between means, and a non-parametric Kruskal Wallis ANOVA was used to compare

variables under the assumption of distinct sample size. Asymmetry of data frequency distribution was reduced by Box-Cox transformation (Sokal & Rohlf 1995) with the software Vernorm (Legendre & Vaudor 1991).

3. Results

3.1. Species ecology

Martiodrilus n. sp. is an endemic anecic earthworm from Carimagua. It is a large size, dorsally dark-grey pigmented, and surface-casting species. Surface casts of Martiodrilus sp. are large and ranged from 3 to 6 cm Ø and from 2 to 10 cm height, with an average dry weight of 25 g (Picture 1). Average monthly fresh cast and total cast numbers were significantly higher ($P < 0.01$, t-test) in the improved pasture than in the native savanna. The number of surface fresh casts declined during the middle of the rainy period due to the fact all the juveniles have already descended to deeper layers to enter diapause. A strong positive correlation between the number of fresh casts and the density of individuals in the first 10 cm was observed in the improved pasture ($r = 0.907$; $P < 0.01$) and it has been proved to be a good estimator of population density.

The highest population density was recorded at the beginning of the rainy season and the new juveniles hatched in October 1994 increase the total number of individuals, despite a reduction in theses numbers due to severe seasonality occurs (Fig. 1). Earthworm biomass ranged from 0.24 g m^{-2} (March 1994) to 8.76 g m^{-2} (September 1995), and from 26.5 g m^{-2} (January 1995) to 94.8 g m^{-2} (May 1994), in the native savanna and in the improved pasture, respectively. In the native ecosystem Martiodrilus sp. comprised 15.1% of total

earthworm biomass,while this value rose to 85.1% in the improved pasture, the highest ever recorded to date for an anecic species. Population density remained stable during the dry season months, therefore it is assumed that mortality occurs during the rainy period and that other factors seem to be responsible for it.

The extremely effective adaptive strategy of Martiodrilus sp. is the reason why there is negligible risk of mortality during the dry season. The species has a true diapause, although different patterns were found between adults and juveniles. The latter were only active during the four months following the onset of the rainy period and entered diapause much earlier than adults, which remained active until December. The cease of activity occurred after they sank to deeper soil layers. An aestivating chamber is built, at the end of its semi-permanent burrow, where they coiled themselves up, after emptying their gut contents. The end of the burrow was usually sealed with several septae to avoid loss of tegumental moisture, which is vital to support a minimal rate of respiration (Picture 2). They remained still until the onset of the next rainy season.

A diapause process, physiologically induced, was assumed to be occurring because in controlled conditions there was no response when aestivating earthworms were introduced into soil with water content near field capacity. Aestivating juvenile earthworms were normally found in the 40- to 50-cm layer, whilst both adults and subadults were located in the 50- to 60-cm layer. A significant non-linear correlation was found between diapausing earthworms weight and the depth at which they were found (Kruskal-Wallis ANOVA, P = 0.011). The larger the individual is the deeper it aestivates (Fig. 2). The average weight of diapausing earthworms ranged from 1 to 2.5 g (4 g maximum), quite low when compared with fresh adult weight, ca. 11.2 g. This is the result of the earthworms emptying their guts to coil themselves up in their aestivating chambers.

The seasonal pattern of vertical distribution for the species is shown in Fig. 3. At the beginning of the rainy period in the first year most of the population was located in the first 20 cm of the soil profile. By the middle of this season, an important proportion of inactive individuals, especially immatures, occupied the deeper soil layers. Adults, on the other hand, were still active in the first 20 cm and entered into the reproductive period. In January 1995, when no stimulus for activity had affected the earthworm community, only some adults and many immatures of Martiodrilus sp. were found in the different soil layers.

Owing to the life cycle of the species, it is a clear K-strategist with a relatively long life period (Jiménez and Decaëns, in preparation). New juveniles emerged from cocoons just before the end of the rainy period rapidly sank towards the deeper horizons to inititiate diapause. In the next year they will become active at the onset of the rainy season and be so during the following 3-4 months (July-August), entering again in a new diapause phase (the weight of these juveniles is 4 g maximum) until the next wet season. At the beginning of the following rainy period (second year) these worms will be active until the middle or the end of the humid season, depending on the developmental stage. In the next year (3rd) these worms become adults and two possibilities must be considered here: i) these new adults will not reproduce until the next year (4th), as some inactive adults were found when no cocoon was collected (see below), or ii) in some years of unusual lower rainfall all reproduction will be initiate by most adults. Adults that constitute, in a given period, the population of Martiodrilus sp., seemed not to actively participate in the reproduction, as the number of adults was double-fold than cocoons. We actually ignore if these adults participated during the reproductive period, but it seems improbable since no cocoons at the onset of the wet season were found (Jiménez and Decaëns, in preparation).

3.2. Effect of Martiodrilus *sp. on soil processes at the scale of biogenic structures*

3.2.1. C and N dynamics in casts

A high nitrogen mineralisation occurred in fresh casts. During the first month of cast ageing the NH_4^+ levels were 5 and 15 times higher in 1-day-old casts than in the bulk soil in the savanna and the pasture, respectively. Afterwards, concentration decreased to a very low and constant value similar to the one observed in the surrounding soil (Fig. 4a, b). It is important to notice that three significant and transient peaks of NO_3^- were successively observed in the casts, the underlying and the adjacent soil (Fig. 4c, d). During the first month, these levels were maintained by the continuous excretion of deposits on the same casts. Then, the earthworms abandoned their burrows and the NH_4^+ concentration progressively fell down to a minimum.

In the soils that had not been recently in contact with earthworms, total C content was significantly higher in the pasture than in the savanna (Fig. 5), while no significant differences were recorded for the total N contents and the C:N ratio). Compared to the bulk soil, casts produced in the two systems had significantly higher C contents (1.5-1.9 times higher) and total N (1.4-1.6 times higher; Fig. 5). The concentrations in total N were rather constant during all the ageing process of casts. But more outstanding and surprising was the continuous and significant increase in C contents observed in casts during their ageing (Fig. 6a, b).

3.2.2. Cast seed banks

Martiodrilus sp. seemed to ingest preferentially large quantities of seeds as part of its diet from 58 to 163 seeds 100 g^{-1} of ingested soil. The percentage of germination of seeds is 3 to 40 times lower in earthworm casts than in soil, probably as a consequence of damages suffered by ingested seeds during gut transit.

In all systems seedlings were observed in casts and only 41% of seeds emerged from casts, and the remaining 59% needed cast destruction to germinate (data not presented Decaëns, unpubl.). In addition, the number of viable seeds within casts were negligible in comparison to soil seed bank and it only accounted for 0.2-0.6% of the total (Fig. 7). However, the total number of seeds collected per 100 g sample was normally higher in casts than in the soil, and the number of viable seeds were greater in the intensive pastures than in the native savanna, and in all systems it was higher in the soil compared with the casts.

Differences were found in the species composition of soil seed banks between both pastures and the savanna, and it was certainly similar in the two pastures. The species composition of the soil seed banks was disimilar to the above ground vegetation, where dominant species did not germinate in greenhouse experiment and on the other hand, the most abundant species of soil seedlings were rare in the plant community. The cast seed bank was relatively closer to that of the standing vegetation than soil seed banks in the native savanna, whilst the opposite pattern was found in B. decumbens and P. phaseoloides pasture.

The number of viable seeds egested in Martiodrilus sp. surface casts is up to 8.7 million seeds. ha^{-1}. yr^{-1}, and from 18 to 878 viable seeds. m^{-2}. yr^{-1} can be egested in surface casts, representing from 1% to 13% of the total viable soil seed bank.

From 64 to 97% of seed viability was lost in earthworm casts, probably due to damages suffered by seed during gut transit, as suggested by the higher percentage of damaged seeds observed in casts.

4. Discussion

4.1. C and N dynamics

Martiodrilus sp. is an endemic species in the well-drained savannas of Carimagua. It may be considered as an anecic species, as defined by Bouché (1972) and Lavelle (1981), being of large size, dorsally pigmented, and litter feeding and surface-casting through opened semi-permanent burrows. Although a more detailed study on its feeding regime has revealed it is not a clear anecic (Mariani et al., 2001).

Casts of Martiodrilus sp. are sometimes large and reach up to 15 cm height and 400 g weight (Jiménez et al., 1998a; Decaëns, 2000). Casts do not dry completely till the earthworm abandons its burrow and the half life of casts ranges between one and three weeks in native and non-native pastures, respectively (Decaëns, 2000). Afterwards, casts are progressively broken until they completely disappear, sometimes by water run-off after a big storm (Decaëns, pers. observ.) or incorporation into the soil profile. The differences in Martiodrilus sp. population density between both systems studied was also perceived by taking into account the number of surface fresh casts (Jiménez et al., 1998b).

Microbial activities and mineralisation are known to be greatly enhanced during gut transit of soil and in fresh casts (Barois et al. 1987). So the high levels of NH_4^+ observed in the fresh casts may be explained by this process together with the addition of urine in the posterior part of the digestive tract (Decaëns et al. 1999a).

The production of NO_3^- in fresh casts via nitrification processes (Scheu 1987; Lavelle and Martin 1992) occurred after the earthworm left its burrow and the NH_4^+ concentration decreased to a minimum. No accumulation of NO_3^- was observed in the casts possibly due to a rapid diffusion into the soil. The hypothesis to explain those three successive peaks in NO_3^- concentrarion may be: (i) a swift production of NO_3^- in the casts followed by diffusion through the gallery by water flowing, and (ii) slower lateral diffusion through the cast and soil surface (Decaëns et al., 1999a). The increasing intensity of the three peaks of NO_3^- may have reflected a stimulation of a nutrient-dependent microflora in the neighbouring soil. Finally, inorganic N excesses largely disappeared from the casts and the surrounding soil. Root uptake, denitrification processes, reorganisation in soil microbial biomass or losses by leaching are factors involved in this process (Syers et al., 1979; Elliott et al., 1990; Lavelle and Martin, 1992).

Casts are known to be stable, rather compact and impermeable when dry (Shipitalo and Protz 1989; Blanchart et al. 1993; Guggenberger et al. 1996). The organic matter they contain is protected efficiently from further decomposition and mineralization processes (Martin 1991; Lavelle et Martin 1992). Slight increases in NH_4^+ and NO_3^- concentrations were observed between 30 and 195 days after the beginning of the experiment, simultaneously in the casts and soil of the two systems (Fig. 4) and can be explained by alternations of dry

and wet conditions that are likely to favour successively NH_4^+ and NO_3^- production in soil (Birch 1964).

During the study period Decaëns et al. (1999a) estimated that, 3 and 34 kg $ha^{-1}.year^{-1}$ inorganic N may be released in fresh casts of Martiodrilus sp., in the savanna and the pasture, respectively (data based on a population density of 0.3 individuals m^{-2} in the savanna and 1.6 individuals m^{-2} in the pasture, Decaëns, unpublished data). But this species also produces underground casts, and the overall production of casts (surface plus below ground) was estimated at 14 t dry casts. ha^{-1}. $year^{-1}$ in the savanna and 114 t. ha^{-1}. $year^{-1}$ in the pasture (calculated after Rangel et al. 1999). Then, a significant contribution to the overall N budget in these agroecosystems derives from the enormous quantities of casts deposited in the soil surface. In the case of the pasture, inorganic N release from casts is equivalent to ≈ 22% of the total annual N uptake by grasses (about 155 kg. ha^{-1}. $year^{-1}$, Fisher and Kerridge 1996). This is also equivalent to ≈ 48% of the total N inputs generally used in upland rice monocultures (70 kg. ha^{-1}. $year^{-1}$, Thomas et al. 1995). This estimates on N mineralisation were consistent with data from the literature (James 1991; Martin 1991; Curry et al. 1995). Moreover, the global contribution of earthworms to N available for plants may have been even higher, due to the presence of significant populations of other species (Jiménez et al. 1998a).

Regarding C dynamics, soil organic C was higher in grass-legume pastures than in the savanna, what agrees with other studies (Thomas et al. 1995).

The capacity of Martiodrilus sp. to select a food substrate with high organic contents (Jiménez et al. 1998b; Rangel et al. 1999), could be the reason why total C and N contents highly significant in casts than in the control soil in both systems (≈ + 100%). Several

factors, the relative importance of which are still unknown, may explain these results although it needs further research (Decaëns et al., 1999a): fixation of atmospheric CO_2 by algae or nitrification bacteria (autotrophic microorganisms); the colonisation of casts by cast-dwelling macroinvertebrates and the accumulation of organic material and/or the production of carbon-enriched faecal pellets (5.2-10.2% of C, Decaëns, unpublished data). Some ants and termites, were found cracking and burrowing casts from 4 to 6 weeks after their deposition in the pasture and the savanna, respectively, and with lower densities than in the surrounding soil (Decaëns et al., 1999b).

A possible effect of the concentration of organic C in the casts and burrows of *Martiodrilus* n. sp. is the build-up of a physically protected and active C pool. The disintegration of the casts leads to the release ot this C that plant could uptake (Lavelle and Martin 1992; Guggenberger et al. 1996). Earthworm-induced C accumulation in stable aggregates may be considerable due to the enormous quantities of soil egested as casts has been estimated at 0.6 t ha^{-1}. $year^{-1}$ and 8.6 t ha^{-1}. $year^{-1}$ in the savanna and the pasture, respectively (Decaëns et al. 1999a). A part of this C (83% and 62% in the savanna and the pasture, respectively) corresponded to the C increase in fresh casts compared with soil, and may have been due to the selective ingestion by earthworms of organic-rich food substrates. The total quantity of C concentrated in the casts of Martiodrilus sp. represented 2 and 30% of the total soil C in the top 10 cm (based on a bulk density of 1.0 g. cm^{-3}), respectively, in the savanna and the pasture (Decaëns et al. 1999a). A similar experiment on C and N dynamics in in-soil casts should clarify the whole process.

4.2. Seed banks

The results of the present study confirm the complex role played by earthworms in the process of seed bank formation and contribution to the above ground vegetation (Willems and Huijsmans 1994). In such systems, the number of viable seeds egested each year in the surface casts of Martiodrilus sp. is important (up to 8.7 million seeds. ha^{-1}. yr^{-1}), compared with results obtained with Lumbricus terrestris L. in temperate pastures (890 thousand seeds. ha^{-1}. yr^{-1} on average) (Willems and Huijsmans 1994). From 18 to 878 viable seeds. m^{-2}. yr^{-1} can be egested in surface casts, representing from 1% to 13% of the total viable soil seed bank.

In our study from 64 to 97% of seed viability is lost in earthworm casts, probably due to damages suffered by seed during gut transit, as suggested by the higher percentage of damaged seeds observed in casts. Earthworm burying activity of seeds may have important consequences for plant community dynamics as seeds of many species survive better buried than when left at the soil surface, and there are few other natural mechanisms that explain how seeds are buried in soil (Grant 1983). Moreover, earthworm faeces may protect seeds from early germination processes and participate in the formation of important and persistent seed banks.

In the savanna protected from fire, casts sometimes remain at the soil surface for more than one year, while burning of the savanna suddenly leads to their destruction by depriving them of the protective effect of the vegetation and litter cover (Decaëns 1999). This may lead to the formation of a pool of seeds potentially ready to germinate, that may be indirectly dispersed by fire on the nearby soil surface where they further benefit from suitable conditions to germinate (*i.e.* bare ground, higher light intensity, available nutrients in ashes). Important chemical constraints on seedling emergence and survival (e.g. low nutrient content, high aluminium saturation) may also be alleviated in casts. Therefore,

seeds in casts, egested at the soil surface may be more likely to germinate than those in the soil seed bank. This can explain why the composition of the cast seed bank was closer to that of the standing savanna vegetation than that at the soil seed bank. Further research shold focus on the effects of earthworm activities in above standing vegetation at larger spatial and temporal scales.

5. Conclusions

Martiodrilus sp. is an endemic earthworm from the natural savannas of Carimagua (Colombia) well adapted to introduced pastures, where it increases its abundance significantly and for instance its effects on some soil processes. The adaptive strategies of earthworms are diverse and are the result of living in a complex environment and facing limiting factors such as poor nutrient contents, movement in a compact environment and sometimes a strong seasonality. This species maintains quite abundant populations in the introduced pastures and its adaptive strategy is extremely efficient to maintain an almost constant density through the dry season.

At Carimagua one earthworm species dominates the macroinvertebrate biomass in the improved pastures and it belongs to the definition of soil ecological engineers via the production of casts and galleries. These structures serve as (i) a trophic resource for other earthworms which ingest the casts, and as physical spaces for certain macro-invertebrates in the interior of galleries or under the casts, (ii) modifiers of the availability and quality of the resource through the modification of the soil structure, organic matter dynamics and nutrient availability to plants, (iii) a means to facilitate the transport of some organisms bringing them be into closer contact with the resource (Decaëns 1999).

The abundance and diversity of biogenic structures are without doubt important for the maintenance of soil functioning in the ecosystem (Lavelle, 1996). A clear example is the complementary effects of compacting earthworms and decompactors (Blanchart et al., 1997). In soils drastically altered where only one compacting species existed, the production of casts resulted in a compaction of the soil, a reduction in rates of water infiltration and a reduction in plant growth (Rose and Wood, 1980; Barros et al., 1998; Blanchart et al., 1999; Chauvel et al., 1999).

In conclusion, the present study confirms the hypothesis of contrasted effects of earthworm activities on soil organic matter, according to the time-scale considered (Martin 1991; Lavelle and Martin 1992; Lavelle et al. 1998). Casts of Martiodrilus sp. may be considered as microsites of short-term mineral N production and medium-term soil organic matter accumulation. Inorganic N production occurs during the period of cast production, and there is evidence of a rapid diffusion of the NO_3^- produced into the surrounding soil. A buil-up of C pool occurs gradually during cast ageing, maybe under the influence of other organisms such as autotrophic microorganisms, small invertebrates and also plant roots. Modifications in the location and dynamics of organic resources through the production of earthworm casts may be considered as an example of the effects of earthworms' "engineering activity" (*sensu* Jones et al. 1994).

Earthworm casts may finally be considered as an important regeneration niche (*sensu* Grubb 1977) for the plant community, and earthworm activity as an indispensable factor of ecosystem sustainability and diversity (Willems and Huijsmans 1994).

Acknowledgements

All this research has been done from a collaboration between CIAT and the IRD institute, and has produced over 24 refeered publications compiled into a CIAT publication [Jiménez and Thomas (Eds.), 2001]. We are indebted to many people who have helped us in these years. We wish to thank CIAT (International Center for Tropical Agriculture, Cali, Colombia), especially to Soil and Plant Nutrition Unit (formerly Tropical Lowlands Program) for human and technical support, and for scientific discussions arised from this research. We also thank Patrick Lavelle (IRD, France), and Richard Thomas, Myles J. Fisher, Edgar Amézquita, Raúl Vera (CIAT) and Dennis K. Friesen (IFDC) for their encouragement and enthusiasm to study the role of earthworms in the savannas and introduced pastures at Carimagua, in the Colombian "Llanos", and the different directors of Carimagua research station during our stay, Jaime Triana and Darío Cárdenas (CORPOICA). The help of Andrés F. Rangel and Alex Cepeda is also appreciated. Useful comments during this research came from our colleagues Jean-Pierre Rossi, Lucero Mariani (IRD). The first author expresses his gratitude to all in the Department of Animal Biology (Invertebrate Zoology) at Universidad Complutense (Madrid, Spain) for support during his Ph. D. Financial support in terms of scholarship, field workers and technical assistance was provided by the EU MACROFAUNA project (overall coordination by P. Lavelle), CIAT and the MAS (Managing Acid Soils) consortium within the Soil Water and Nutrient Management systemwide program (SWNM). Thanks to Michel Brossard (IRD-EMBRAPA Brasilia) for inviting the first author to the International Symposium on Soil Functioning under Pastures, and two anonymous referees for useful and precise comments on the manuscript. Finally, our deepest and most sincere gratitude to the field workers for their excellent work and their friendship and to the kindly local people in the "Llanos". Both of us were very fortunate in doing our field Ph.D research in such a beatiful area where fascinating and outstanding landscapes ("esteros", "morichales" and red skies) and still a wild fauna were our daily privileges.

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Figure captions

Figure 1. Density and biomass (± S.D.) of *Martiodrilus* n. sp. in the native savanna and *B. decumbens* + Kudzu pasture (Figure from Jiménez et al., 1998a).

Figure 2. Relationship between the vertical distribution in the soil profile of aestivating individuals of *Martiodrilus* n. sp. and their weight (Figure from Jiménez and Decaëns, 2000).

Figure 3. Vertical distribution of *Martiodrilus* n. sp. in the introduced pasture in May 1994 (a), July 1994 (b), November 1994 (c) and January 1995 (d). (Figure from Jiménez et al., 1998a).

Figure 4. Evolution over time of NH_4^+ and NO_3^- contents in the soil and the casts of the *B. humidicola / A. pintoi* pasture (**a, c**) and the native savanna (**b, d**) (From Decaëns et al., 1999a)

Figure 5. Mean values of total C (a), total N (b) and C:N ratio (c) in the soil and the casts of the two systems studied (*different letters* mean significant differences at $P < 0.05$). ppm $\mu g\ g^{-1}$

Figure 6. Evolution over time of the total C in the soil and the casts of the *B. humidicola / A. pintoi* pasture (a) and the native savanna (b). (Adapted from Decaëns et al., 1999a).

Figure 7. Density of germinable seeds contained in soil (a) and casts (b) in the three systems. Bars indicate standard errors; letters mean differences at $P < 0.05$ (t test).

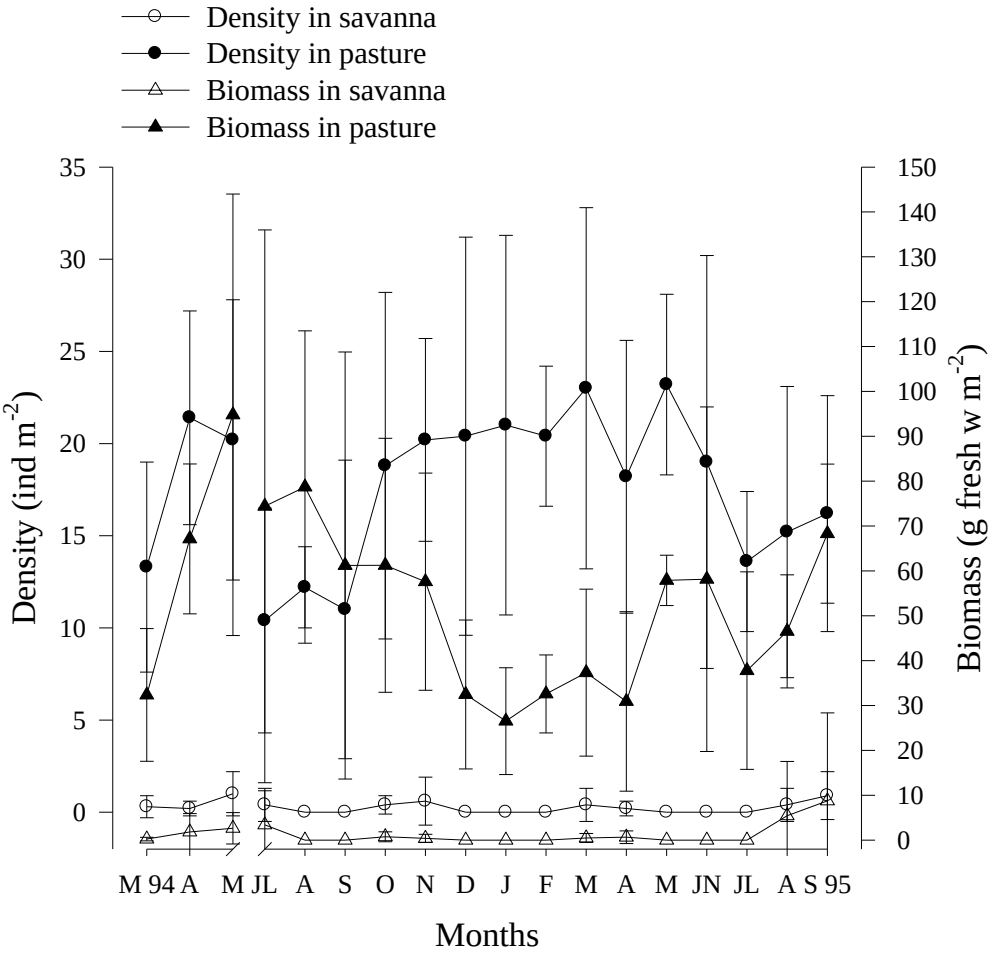

Density in savanna
Density in pasture
Biomass in savanna
Biomass in pasture
Density (ind m-2)
Biomass (g fresh w m-2)
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
M 94 A M JL A S O N D J F M A M JN JL A S 95
Months

Figure 1

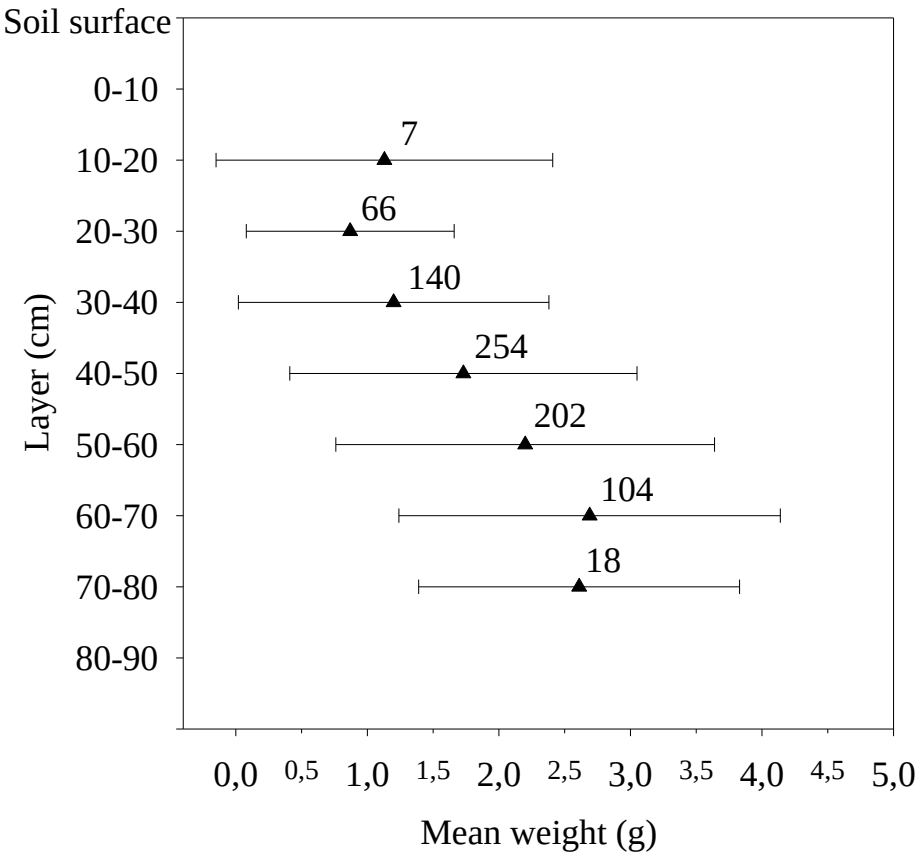
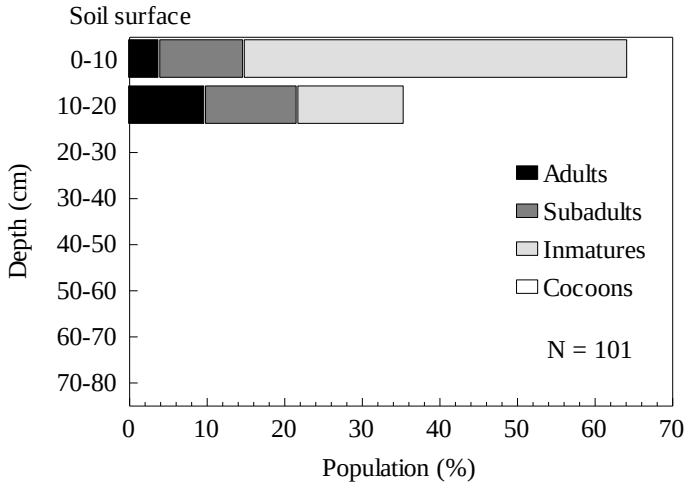
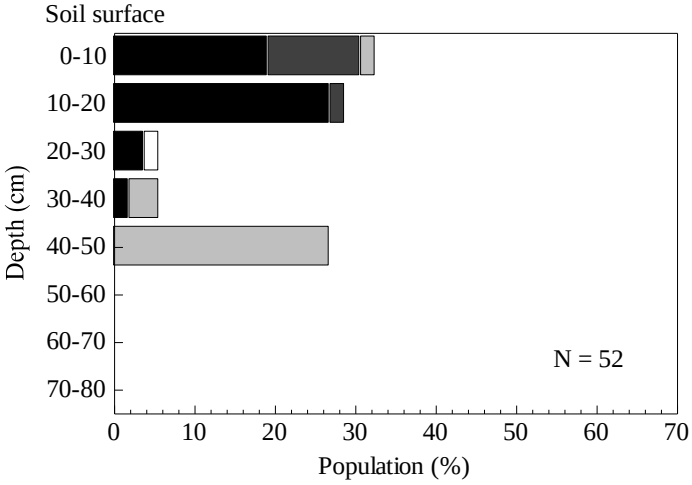

Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
Layer (cm)
7
66
140
254
202
104
18
0,0
0,5
1,0
1,5
2,0
2,5
3,0
3,5
4,0
4,5
5,0
Mean weight (g)

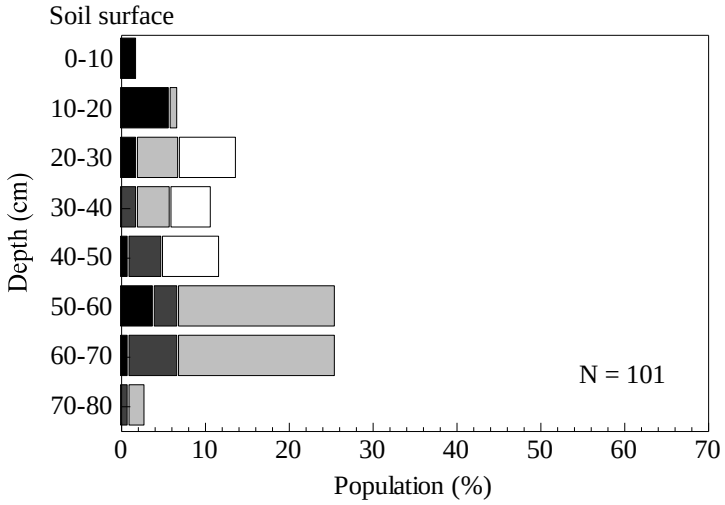
Figure 2.

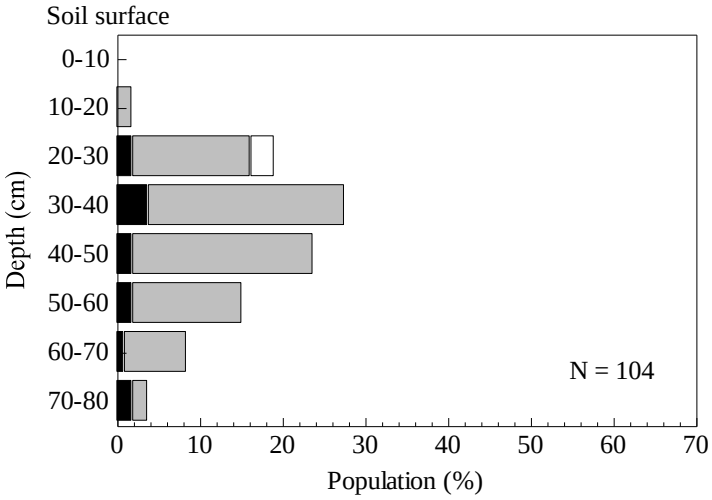

Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Depth (cm)
Adults
Subadults
Inmatures
Cocoons
N = 101
0
10
20
30
40
50
60
70
Population (%)

a)


Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Depth (cm)
N = 52
0
10
20
30
40
50
60
70
Population (%)

b)


Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Depth (cm)
N = 101
0
10
20
30
40
50
60
70
Population (%)


Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Depth (cm)
N = 104
0
10
20
30
40
50
60
70
Population (%)

d)

c)

Figure 3.

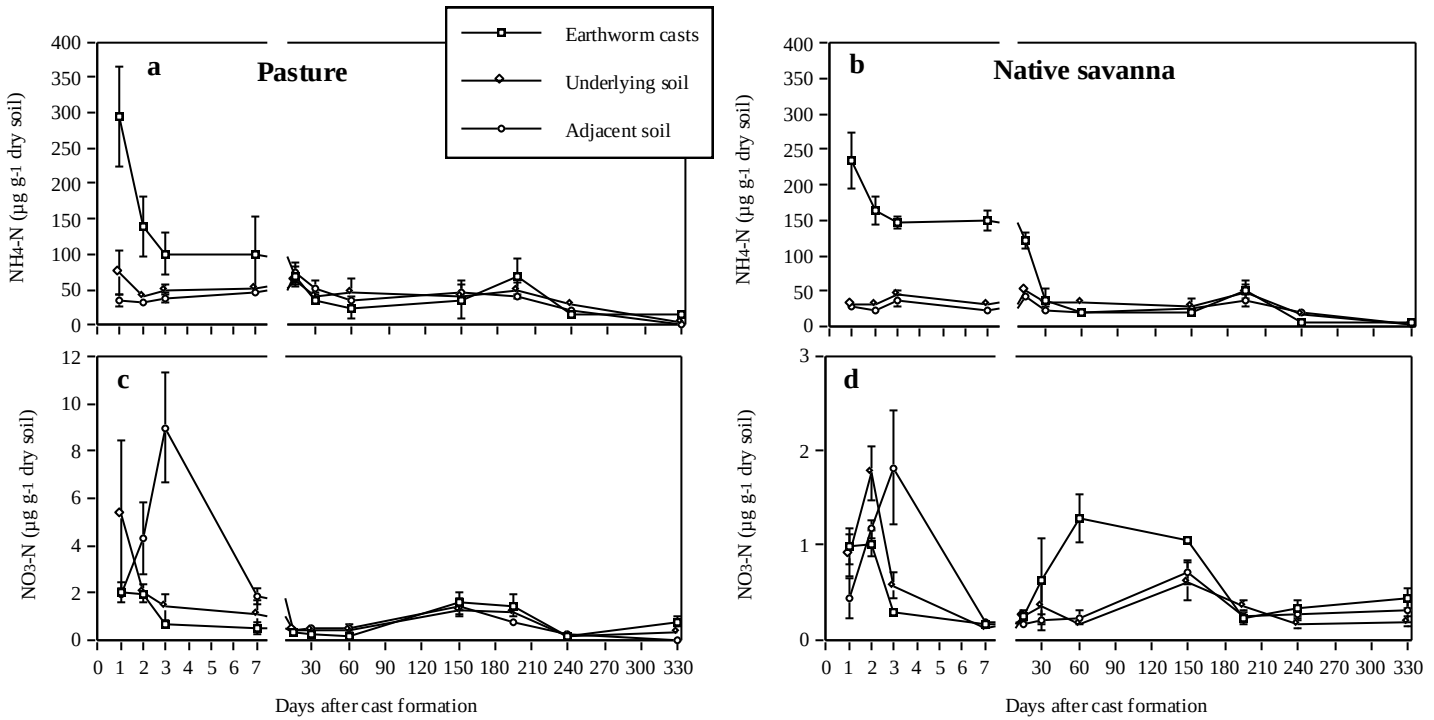

a
Pasture
b
Native savanna
c
d
Earthworm casts
Underlying soil
Adjacent soil
NH4-N (µg g-1 dry soil)
NO3-N (µg g-1 dry soil)
Days after cast formation
0 1 2 3 4 5 6 7 30 60 90 120 150 180 210 240 270 300 330

Figure 4.

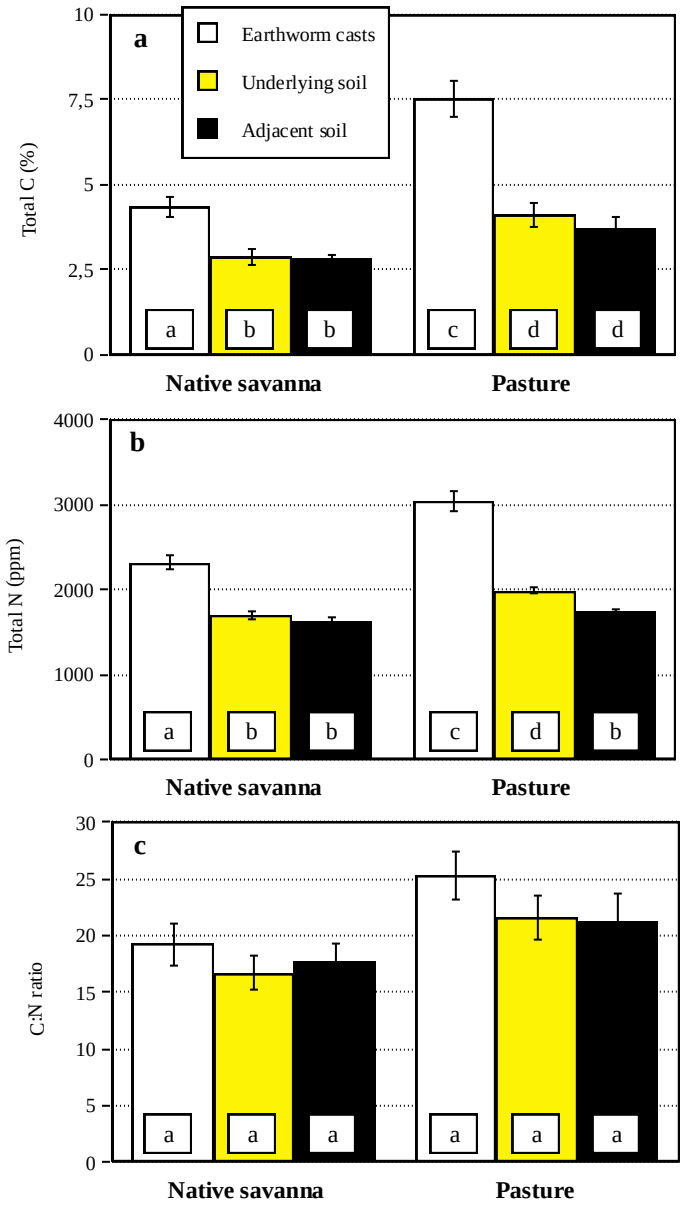

a
Earthworm casts
Underlying soil
Adjacent soil
Total C (%)
10
7,5
5
2,5
0
a
b
b
c
d
d
Native savanna
Pasture
b
Total N (ppm)
4000
3000
2000
1000
0
a
b
b
c
d
b
Native savanna
Pasture
c
C:N ratio
30
25
20
15
10
5
0
a
a
a
a
a
a
Native savanna
Pasture

Figure 5.

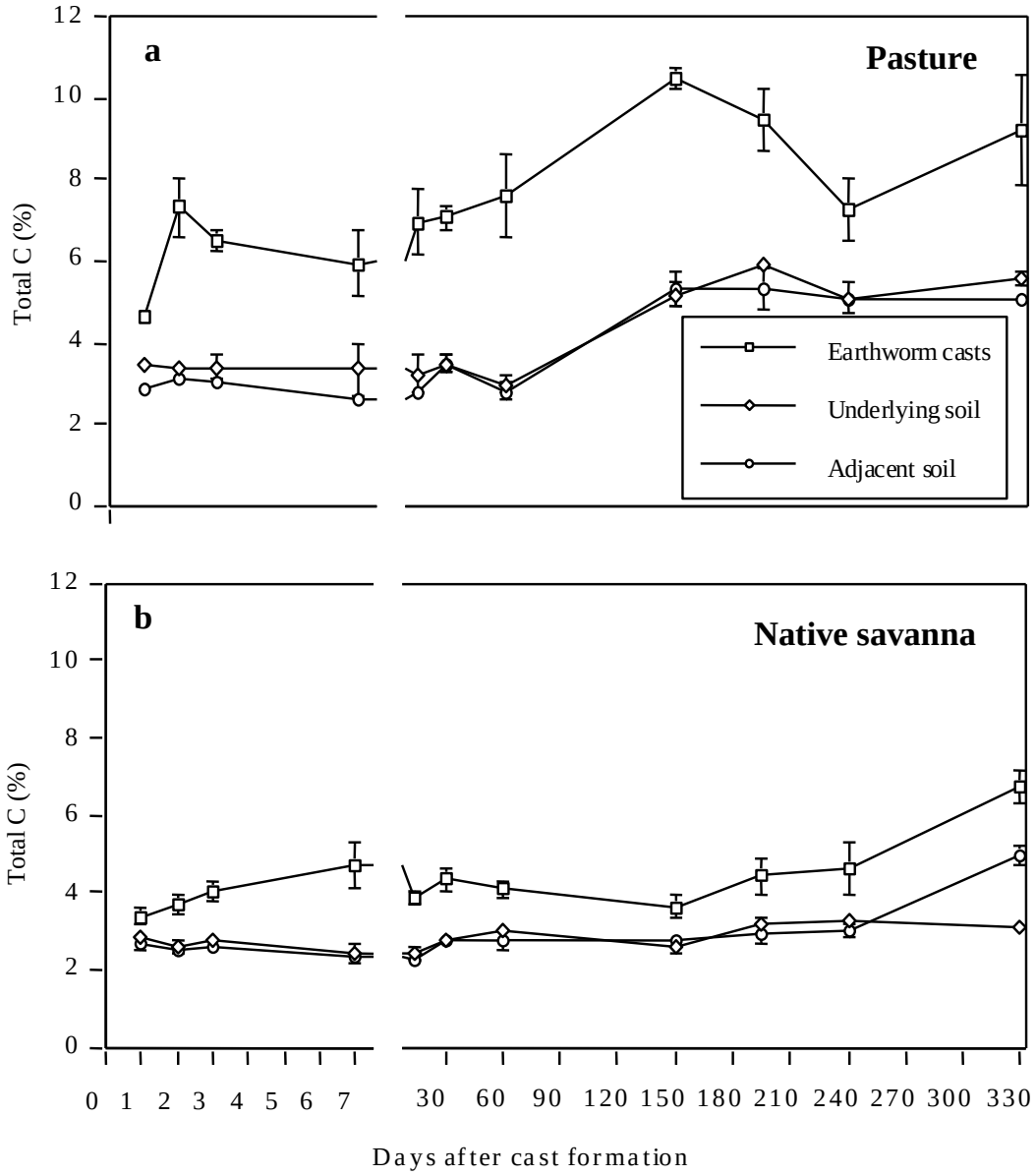

a
Pasture
b
Native savanna
Total C (%)
Earthworm casts
Underlying soil
Adjacent soil
Days after cast formation

Figure 6.

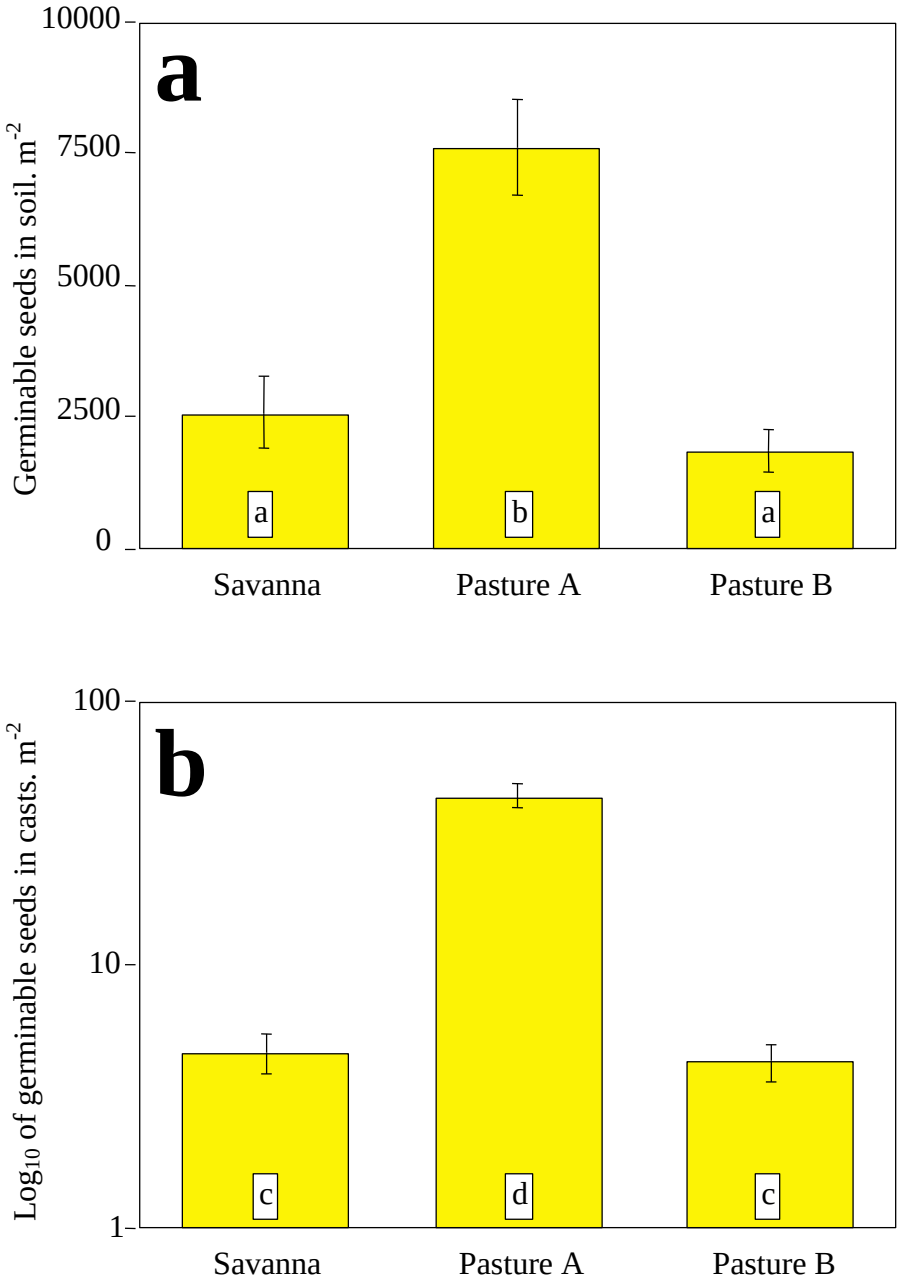

a
10000
7500
5000
2500
0
Germinable seeds in soil. m-2
a
b
a
Savanna
Pasture A
Pasture B
b
100
10
1
Log10 of germinable seeds in casts. m-2
c
d
c
Savanna
Pasture A
Pasture B

Figure 7.

Scheme 1. Turricule of *Martiodrilus* n. sp. in the natural savanna from Carimagua (scale: length of picture = 20 cm) (photo: T. Decaëns).

Scheme 2. Pattern of diapause in *Martiodrilus* n. sp. with the aestivation chamber at the end of the burrow (dotted line) and the septae (arrows) built with cast material (photo: J.J. Jiménez).